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SEASONAL ACTIVITY OF BOREAL FOREST-FLOOR SPIDERS (ARANEAE)

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ABSTRACT. We studied the seasonal occurrence of forest-floor spiders by collecting samples with 100 pitfall traps operated throughout the growing season of 1985 in a mature coniferous stand in southern Finland. Samples were collected at five-day intervals in May-August and at longer intervals in September-November. The entire sample from the 26 trapping periods consisted of 6753 adult spiders of 100 species. The overall abundance and species richness was highest in the early season, May and June. Seasonal spider catch was not correlated with fluctuations in temperature, but was negatively correlated with rainfall. Nine of the ten abundant species ($\geq$2% of the sample each) belonged to the family Linyphiidae (*sensu lato*) and one to the family Agelenidae. *Macrargus rufus* (Wider) was the most abundant species comprising approximately ⅓ of the sample followed by *Lepthyphantes alacris* (Blackwall) (17% of the sample). The activity peaks of the ten abundant species were usually short, only a few weeks, and occurred in the early and mid-season, May–July. Only *L. alacris* was collected every trapping period. Although numbers of males clearly exceeded that of females in most species, the seasonal occurrence of the sexes coincided. Our results differ somewhat from earlier observations about spider phenology in Finland. It is possible that this discrepancy depends to a great extent on different sampling methods used.

Conservation issues in boreal forests have drawn growing attention in ecological discussions since the 1980's (e. g., Bonan & Shugart 1989; Mikkola 1991; Hansson 1992; Niemelä et al. 1993, 1994a). This concern arises from the observation that in many parts of the world natural boreal forests are threatened by the expanding forestry activities (Korsmo 1991; Boyle 1992; Haila 1994). Consequently, there is a burning need for ecological information about species in boreal forests to serve as baseline data in assessment of their response to forestry practices (Haila et al. 1987, 1994; Niemelä et al. 1988, 1994b; Esseen et al. 1992).

In spite of its apparent monotony, the boreal forest includes several 'subsystems' of which the litter layer with its decomposer arthropods is an important one. On the forest floor, spiders (Araneae) are an ecologically significant group (Jennings et al. 1988) because of their role in regulating decomposer populations (Clarke & Grant 1968). Therefore, possible changes in spider assemblages following forestry practices are of importance to the whole arthropod fauna of the forest floor (McIver et al. 1992). The estimation of these effects is hampered, however, by the insufficient knowledge of many basic life-history features of boreal forest spiders. In this study we focus on one such feature of these spiders: their seasonal activity pattern. Adult activity period is an important life stage and thus merits description. Our phenology description is based on pitfall samples collected continuously throughout the growing season in a mature coniferous forest in Finland. We also compare our findings with results of previous, more heterogeneous data.

METHODS

Study area.—The spiders were collected from the Musturi State Forest Reserve (area about 19 ha) in northern Häme, *ca.* 8 km SW of the Hyytiälä Forestry Station (*ca.* 62°N, 24°E). The study area is located on the border between the southern boreal and middle boreal phytogeographical zones (Ahti et al. 1968). In Musturi, the dominant tree is Norway spruce (*Picea abies*), with some interspersed Scots pine (*Pinus silvestris*), aspen (*Populus tremula*), birch (*Betula* spp.) and mountain ash (*Sorbus aucuparia*). The canopy spruces are mostly over 140 years old, and their mean height is 24 m, mean basal area 37 m^2/ha, and canopy cover 90%. Abundant herbaceous plants include *Vaccinium myrtillus*, *V. vitis-idae*, *Deschampsia flexuosa*, *Linnea borealis*, *Maianthemum bifolium*, and mosses *Dicranum* spp., *Pleurozium schreberi*, *Polytrichum* spp. The study site is described in more detail by Niemelä et al. (1989, 1992).

Sampling design.—To collect the spiders we

Table 1.—Spider catch, number of species and the value of Hurlbert's (1971) diversity index Δ_1 during the 26 sampling periods in the Musturi forest in 1985. Catches and species number from September through November are standardized to 5 trapping days which was the length of the trapping period earlier in the season. Sampling was started on 11 May.

Sample collected	Spider catch	Species number	Δ_1
May 16	962	24	0.52
May 21	483	18	0.63
May 26	74	10	0.74
May 31	867	33	0.85
June 5	327	32	0.86
June 10	374	28	0.86
June 15	280	29	0.87
June 20	205	34	0.85
June 25	397	37	0.79
June 30	273	27	0.73
July 5	434	37	0.80
July 10	429	35	0.80
July 15	494	40	0.80
July 20	156	20	0.72
July 25	96	17	0.73
July 30	119	12	0.67
August 4	24	5	0.66
August 9	45	9	0.68
August 14	36	11	0.84
August 19	68	17	0.85
August 24	88	20	0.82
August 29	97	21	0.82
September 8	27	10.3	0.86
September 23	24	9.1	0.86
October 23	32	12.5	0.90
November 23	19	7.7	0.79

used 100 pitfall traps (plastic cups, diameter 65 mm and volume 170 ml) placed *ca.* 5 m apart in a grid of 4 × 25 traps. They were partially filled with water and NaOH during the 5-day trapping periods in the summer, and with ethylene glycol during the longer trapping periods in the autumn. To keep out rainwater, and to keep avian and mammalian predators from the traps, we placed small metal roofs (10 × 10 cm) a few centimeters above the traps.

Trapping started on 11 May and ended on 23 November 1985. It covered the whole growing season (permanent daily mean temperature >5 °C) which lasted in the study area from 6 May through 26 October (Finnish Meteorological Institute 1985). The traps were serviced every 5 days until 29 August, and thereafter on 8 September, 23 September, 23 October and 23 November. We used temperature and rainfall data from the meteorological station at the Hyytiälä Forestry Station 8 km from Musturi (Finnish Meteorological Institute 1991) to study the relationship between temperature and rainfall, and spider catch.

Pitfall trapping is a widely used method for sampling ground-living spiders (e. g., Tretzel 1954; Duffey 1962; Koponen 1972, 1976; Granström 1973; Westerberg 1977; Curtis 1980; Hauge & Wiger 1980; Niemelä et al. 1986; Itämies and Jarva-Kärenlampi 1987, 1989; Jennings et al. 1988; McIver et al. 1992; Topping 1993). As pitfall-trap catches may better indicate spider activity than density (Topping & Sunderland 1992), we make no statements about density variation

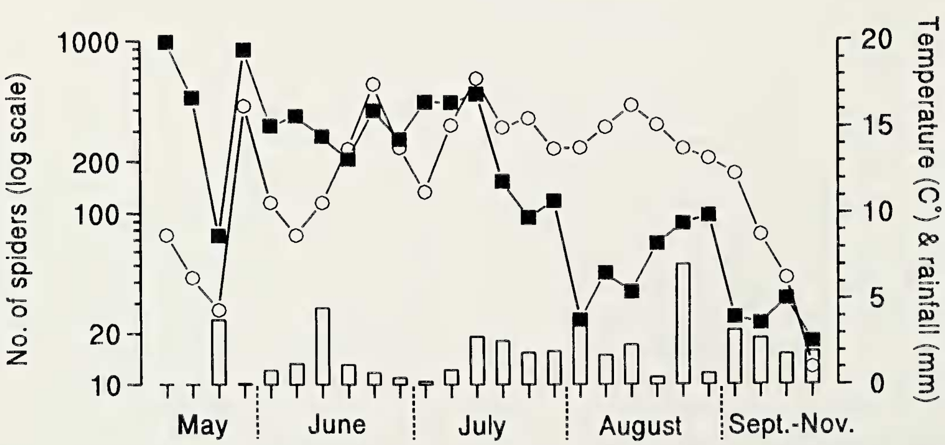

Figure 1.—Number of spiders (black squares) collected, the five-day mean temperatures (open circles), and the total rainfall (bars) during the 26 trapping periods in Musturi in 1985. In September-November the figures are standardized to five trapping days, which was the length of the trapping period earlier in the season.

Table 2.—Spearman rank correlation (R_s) and its statistical significance (P) between the seasonal catches of males and females for the ten most abundant species. In addition, total catches of the species in May 1985, from September through November 1985, and from December 1985 through early May 1986 are given.

	R_s	P	May 1985	Sept–Nov. 1985	Dec.–May 1985–86
Linyphiidae					
Agyneta conigera	0.80	<0.001	0	1	0
A. ramosa	0.69	<0.001	0	0	0
Centromerus arcanus	0.42	0.034	17	5	15
Lepthyphantes alacris	0.75	<0.001	589	88	245
L. antroniensis	0.46	0.019	71	0	17
L. tenebricola	0.82	<0.001	0	42	2
Macrargus rufus	0.24	0.243	1018	72	282
Erigonidae					
Diplocentria bidentata	0.54	0.005	36	1	9
Tapinocyba pallens	0.81	<0.001	61	2	14
Agelenidae					
Cryphoeca silvicola	0.66	<0.001	280	3	38

but focus on species-specific seasonal activity patterns. Although species are expected to vary in their tendency to be trapped (e. g., Heydemann 1961, Huhta 1971), we assume that the species-specific trappabilities remain stable enough throughout the season to warrant comparisons within species.

We used Hurlbert's (1971) index Δ_1 to study species diversity during the trapping season:

$$\Delta_1 = (N/N - 1)\left(1 - \sum_{i=1}^{S} \Pi_i^2\right)$$

where N = total number of individuals in the sample, N_i = the number of individuals of the ith species in the sample, $\Pi_i = N_i/N$, S = the number of species in the sample. Index values range from 0 (low diversity) to 1 (high diversity).

RESULTS

The spider assemblage.—The total spider sample from Musturi comprised 6753 adult individuals of 100 species. The catches were highest in May and decreased thereafter towards autumn (Table 1, Fig. 1). From mid-July onwards the catches decreased rapidly and in August were only about $\frac{1}{10}$ of the peak abundance in the early season. Species richness showed a slightly different pattern with a low in May, and high from late May through mid-July (Table 1). In addition, there was a smaller peak in late August. Species diversity, Hurlbert's (1971) index Δ_1, was lowest in May, increasing rapidly thereafter. The index value remained high through the rest of the season except for a low in late July and early August (Table 1).

During May the spider catch appeared to follow fluctuations in the five-day mean temperatures at the nearby Hyytiälä Forestry Station (Fig. 1). Very low catch in the third trapping period in May was caused by cold weather. However, later on the close correlation between spider catch and temperature disappeared; and there was no correlation between the spider catch and the temperature across the season (Spearman rank correlation R_s = 0.20, ns, n = 26). We calculated Spearman rank correlations separately for early part of the season (May 11–July 15) and for the late season (July 20–November 23) to examine whether the response of spiders to temperature changes during the summer, but there were no statistically significant correlations (R_s = 0.25, P = 0.410, n = 13, and R_s = 0.47, P = 0.104, n = 13 for early and late season, respectively). However, a significantly negative correlation was detected between spider catches and rainfall across the season (Spearman rank correlation R_s = −0.57, P = 0.002, n = 26). There was no correlation between temperature and rainfall (R_s = −0.02, P = 0.917, n = 26).

Forest floor spiders can be roughly divided into two 'guilds' based on their foraging behavior: visual-pursuit hunting species, and microweb-building species (e. g., Huhta 1971; Pajunen 1988; McIver et al. 1992). In our data, species richness of web-spinning species was much high-

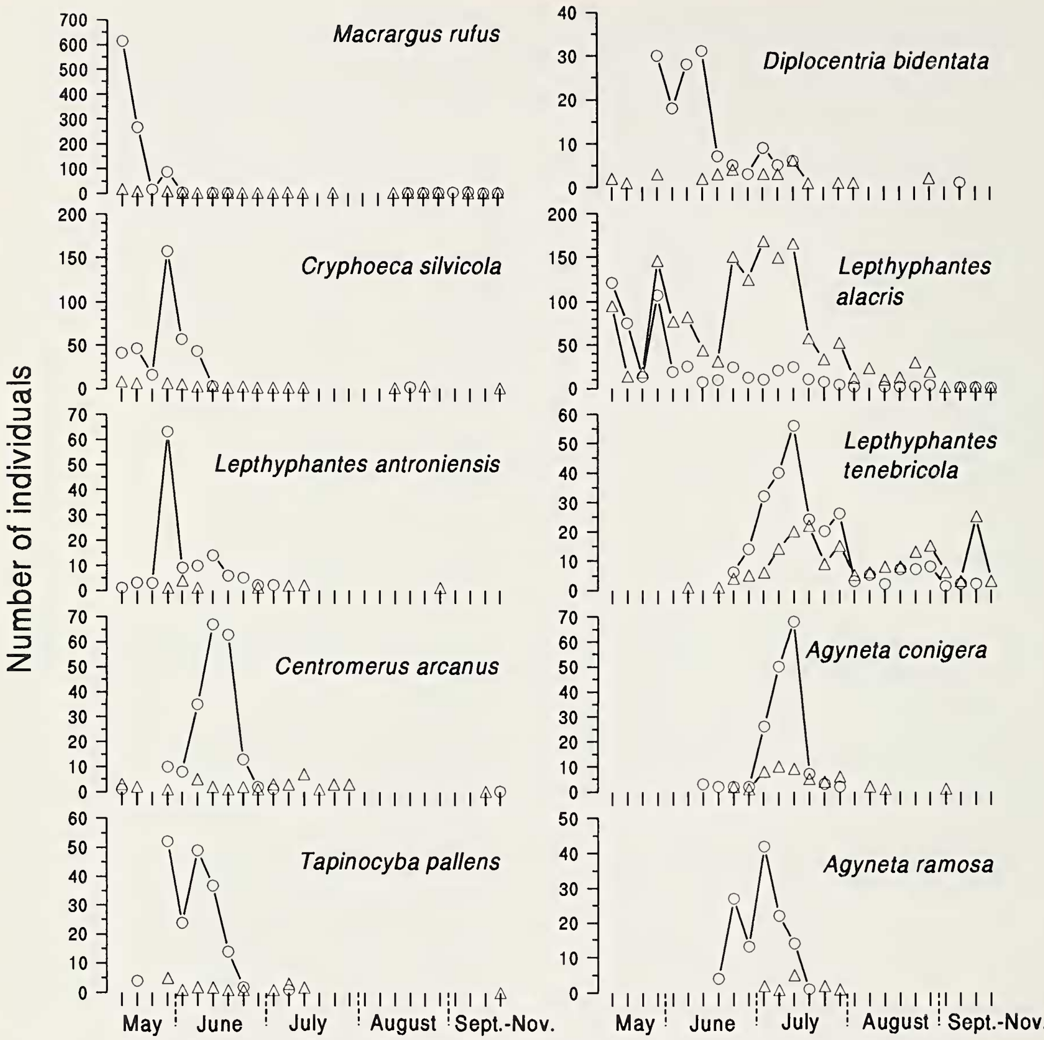

Figure 2.—Number of females (triangles) and males (circles) of each of the ten most abundant spider species (each ≥ 2% of the catch) collected during the 26 trapping periods in Musturi in 1985. Samples from September through November are standardized to five trapping days which was the length of the trapping period earlier in the season. Note the different scales of the vertical axes.

er (73 species) than that of hunting spiders (27 species). Of the 10 abundant species treated separately below, only one (*Cryphoeca silvicola* (C. L. Koch)) was probably a hunting spider; all others being web-builders. These two 'guilds' had similar seasonal activity patterns.

Activity patterns of the species.—Ten species dominated the sample (≥2% of the catch each) and made up 77% of the total catch. *Lepthyphantes alacris* (Blackwall) and *Macrargus rufus* (Wider) constituted almost half (48%) of the catch and they were 4.7 and 2.5 times more numerous, respectively, than the third most abundant species *Lepthyphantes tenebricola* (Wider). In addition to these ten species, another 17 species were fairly numerous (≥26 individuals, i. e., on average ≥1 specimens per trapping period) and accounted for 17% of the catch (species are listed in Table 3). The great majority of the species (73 species) were occasional, being represented by a total of 435 individuals (6% of the catch).

Most of the abundant spider species showed a short activity peak of only a few weeks during the season (Fig. 2). Many species peaked early in the season (May–June), some in the middle (July), but none in the later part of the growing

Table 3.—Catches of the 17 less abundant species (≥26 individuals in total) by month in Musturi. The catches are standardized to 20 trapping-days and rounded to closest integer; 0 < 0.5, — = not collected.

	May	June	July	August	Sept.	Oct–Nov.	Total
Linyphiidae							
Microneta viaria	18	21	11	1	—	0	51
Agyneta subtilis	1	25	41	—	—	—	67
Oreonetides vaginatus	8	15	3	—	—	0	26
Allomengea scopigera	—	—	—	43	26	7	76
Drapetisca socialis	—	—	—	1	7	6	14
Helophora insignis	—	—	—	3	2	9	14
Porrhomma pallidum	7	3	9	3	1	4	27
Erigonidae							
Trichopterna mengei	78	8	15	3	2	1	107
Walckenaeria cucullata	31	35	2	—	—	—	68
W. cuspidata	42	10	1	1	1	1	55
W. dysderoides	—	17	6	—	—	0	23
W. obtusa	13	31	3	—	1	0	48
W. antica	13	9	1	1	—	0	24
Dicymbium tibiale	22	25	12	—	—	—	59
Lycosidae							
Pardosa lugubris	1	37	29	3	—	—	70
Therididae							
Robertus lividus	—	15	17	—	1	2	35
Gnaphosidae							
Haplodrassus soerenseni	—	32	25	—	—	—	57
Total	233	283	175	59	41	30	821

season (August onwards). For most species the activity is almost entirely due to males, and numbers of males clearly exceeded that of females in all species except *L. alacris* (Fig. 2). The seasonal occurrence of the sexes coincided for all species except *M. rufus*, which was very abundant the first trapping period but disappeared rapidly from the samples thereafter (Table 2).

Lepthyphantes alacris was the only species collected every trapping period, whereas its congener, *Lepthyphantes tenebricola* (Wider) did not appear until in June (Fig. 2). Similarly, *Agyneta conigera* (O. P.-Cambridge) and *Agyneta ramosa* Jackson did not appear until mid-June, and peaked shortly from late June through mid-July.

C. arcanus, *L. alacris*, *L. antroniensis*, *M. rufus*, *T. pallens*, and *C. silvicola* that peaked in the early season had fairly high catches the following May in traps that were operated throughout the winter and collected right after snow-melt (Table 2). This observation confirms our finding that these species indeed are active in the early season. Species peaking later in the season (*A. ramosa*, *A. conigera*, *D. bidentata*, *L. tenebricola*) did not have especially high catches in the sample collected the following spring.

Due to small catches, it was necessary to pool the catch of each of the 17 less abundant species by month. Thirteen of these species occurred predominantly in the early and mid-season, May–July (Table 3). Three species occurred in the late season (August onwards) and one occurred throughout the season. Some congeneric species tended to have similar seasonal occurrence. For instance, all *Walckenaeria* species occurred predominantly in the early season and *Agyneta* species in the mid-season (Table 3, Fig. 2). However, each of the three abundant *Lepthyphantes*-species showed quite a different activity pattern.

The results presented above were based on a one-year study, but we have collected additional data from the same site in the years 1986–1989, and we can thus estimate the reliability of our observations in 1985. As the samples were collected less frequently in 1986–1989 (every four weeks) and using fewer traps (64) the resulting pattern of seasonal occurrence is not as detailed as in 1985. However, a comparison among the

Table 4.—Monthly catches of the ten most abundant spider species in 1985–1989.

		May	June	July	August	Total
Macrargus rufus	1985	1018	21	9	12	1060
	1986	3	16	15	2	36
	1987	416	14	2	3	435
	1988	252	24	11	4	291
	1989	67	11	15	7	100
Cryphoeca silvicola	1985	280	117	3	4	404
	1986	4	0	0	0	4
	1987	147	29	0	1	177
	1988	39	3	0	1	43
	1989	21	1	0	0	22
Lephthyphantes antroniensis	1985	71	52	6	1	130
	1986	3	1	0	0	4
	1987	10	6	0	0	16
	1988	1	0	0	0	1
	1989	1	1	1	0	3
Centromerus arcanus	1985	17	199	21	0	237
	1986	57	10	0	0	67
	1987	12	88	2	1	103
	1988	33	8	0	0	41
	1989	73	42	3	4	122
Tapinocyba pallens	1985	61	133	7	0	201
	1986	2	0	0	0	2
	1987	2	6	0	0	8
	1988	1	0	0	0	1
	1989	4	2	0	0	6
Diplocentria bidentata	1985	36	101	34	3	174
	1986	4	1	1	0	6
	1987	5	17	2	1	25
	1988	0	1	0	1	2
	1989	15	3	5	4	27
Lephthyphantes alacris	1985	589	604	698	109	2000
	1986	52	122	134	11	319
	1987	125	99	96	9	329
	1988	39	70	22	26	157
	1989	327	329	227	19	902
Lepthyphantes tenebricola	1985	0	31	284	87	402
	1986	0	7	18	1	26
	1987	0	15	24	7	43
	1988	0	40	29	47	116
	1989	0	12	21	22	55
Agyneta conigera	1985	0	12	198	3	213
	1986	0	23	12	0	35
	1987	0	1	14	0	15
	1988	0	3	0	0	3
	1989	0	15	8	0	23
Agyneta ramosa	1985	0	44	90	0	134
	1986	11	52	1	0	64
	1987	1	49	12	0	62
	1988	0	18	0	0	18
	1989	0	32	2	0	34

Table 5.—The time of highest catch of the ten most abundant species in our data and according to Palmgren (1972) and Huhta (1965, 1971). Early season includes April–May, mid-season June and July, and late season August–November. However, Palmgren (1972) does not define the seasons using months. (—) indicates that the species was not collected or was so rare that no inferences about phenological occurrence can be made.

	Present study	Palmgren (1972)	Huhta (1965, 1971)
Linyphiidae			
Macrargus rufus	early season	increasing toward late season	increasing toward late season
L. alacris	early to mid-season	early and mid-season	—
L. antroniensis	early season	—	—
L. tenebricola	mid to late season	early to mid-season	—
Centromerus arcanus	early season	early and late season	throughout the season, low in July and August
Agyneta conigera	mid-season	early and mid-season	—
A. ramosa	mid-season	mid-season	—
Agelenidae			
Cryphoeca silvicola	early season	throughout the season	—
Erigonidae			
Tapinocyba pallens	early season	early and late season	throughout the season, low in June and July
Diplocentria bidentata	early season	late season	throughout the season, low in August

years indicated that the seasonal activities of the species were similar in 1985 and in the later years despite great variation in catches among the years (Table 4).

DISCUSSION

The sample from Musturi was quite similar to a pitfall sample from a survey of 24 mature forest fragments in northern Häme in 1984 (Pajunen 1988). The short trapping period (five days in early June) in the fragment survey may at least partly explain their low species richness (70 species) as compared to Musturi (100 species). Most of the 22 species collected in Musturi but not in the survey occurred after June. Only 11 species collected in the survey were not found in Musturi. The most numerous species in both data sets was *L. alacris*, and a majority of the abundant species were common to Musturi and the survey. Thus, the spider assemblage in Musturi is representative of the spider fauna of southern and central Finnish boreal forest. Furthermore, in the Musturi assemblage, the clear numerical dominance of web-building spiders (*ca.* 90% of the catch) over hunting spiders is typical in mature boreal forest (e. g., Huhta 1965, 1971; Palmgren & Biström 1979; Väisänen and Biström 1990), and also in subarctic pine and birch forest in (Koponen 1975, 1976).

In our study, the maximum of spider activity and species richness occurred from May through early July. A similar pattern of high activity in the early season was reported for carabids in Musturi (Niemelä et al. 1989). It has been shown that carabids are most active during the reproductive period (Loreau 1985), and this has been suggested for spiders as well (Huhta 1965). For carabids, Niemelä et al. (1989) hypothesized that perhaps the short growing season of the north drives species into early reproduction, resulting in concomitant high adult activity, thus giving the larvae enough time to complete their development or reach the right larval stage for overwintering. A similar explanation may apply to spiders and is strongly suggested by the prevalence of male spiders in the traps.

Palmgren (1972) divided spider species from different habitats in southern Finland into 13 types by seasonal occurrence. The most predominant type in Palmgren's (1972) classification was species peaking in early season: such species constituted about one third of his 227 classified species. The seasonal occurrence of some species was also analyzed by Huhta (1965, 1971).

Our findings of seasonal occurrence corresponded fairly well to those reported by Huhta (1965, 1971) and Palmgren (1972) for *L. alacris*, *C. arcanus*, *T. pallens*, *A. conigera* and *A. ra-*

mosa. However, for *M. rufus*, *C. silvicola*, *D. bidentata* and *L. tenebricola* our results differed from those reported by Palmgren and Huhta (Table 5). *L. antroniensis* was not reported by Huhta (1965, 1967) or Palmgren (1972). These discrepancies in seasonal occurrence may in part be explained by the different sampling methods used. Pitfall trapping is based both on activity and abundance of the spiders (Topping & Sunderland 1992), whereas litter extraction used by Huhta (1965, 1971) and sieving of litter by Palmgren (1972) record specimens present in the litter at the time of sampling. As time of highest activity and highest density may not coincide, these two methods may give different results in terms of seasonal occurrence (Huhta 1971; Topping & Sunderland 1992). In addition, litter sampling may underestimate spider densities during the activity peaks because mobile and large specimens are not easily captured by these methods (Heydemann 1961). On the other hand, the seasonal occurrence of the four species (*A. conigera*, *D. bidentata*, *L. tenebricola*, *L. alacris*) trapped by pitfalls in our study and by Koponen (1976) in Lapland was similar. Furthermore, high spider activity and species richness in the early season was reported from pitfall samples from spruce forests in Maine (Jennings et al. 1988), and from grasslands in England (Duffey 1962; Topping & Sunderland 1992).

It is worth noting that the seasonal patterns of the same species in Palmgren's (1972) study from the southern coast of Finland and in Huhta's (1965, 1971) studies from forests in central Finland were fairly similar (Table 5) indicating that species phenology remains constant in different geographical areas. This observation also implies that the dissimilarity of our results with Huhta's and Palmgren's observations was indeed due to different sampling methods.

To conclude, there was a great deal of variation in the seasonal occurrence of spiders and in species richness over the growing season in our study forest. However, the seasonal activity patterns remained similar through several years indicating that our observations are representative of mature, spruce-dominated taiga of the southern boreal zone.

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LITERATURE CITED

Ahti, T., L. Hämet-Ahti, & J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn., 5:169–211.

Bonan, G. B. & H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst., 20:1–28.

Boyle, T. J. B. 1992. Biodiversity of Canadian forests: current status and future challenges. Forestry Chronicle, 68:444–453.

Clarke, R. D. & P. R. Grant. 1968. An experimental study of the role of spiders in a forest litter community. Ecology, 49:1152–1154.

Curtis, D. 1980. Pitfalls in spider community studies (Arachnida, Araneae). J. Arachnol., 8:271–280.

Duffey, E. 1962. Population study of spiders in limestone grassland. J. Anim. Ecol., 31:571–599.

Esseen, P.-A., B. Ehnström, L. Ericson, & K. Sjöberg. 1992. Boreal forests - the focal habitats of Fennoscandia. Pp. 252–325, *In* Ecological principles of nature conservation, applications in temperate and boreal environments. (L. Hansson, ed.). Elsevier, London.

Finnish Meteorological Institute. 1985. Ilmastotietoja termisestä kasvukaudesta 1985, ilmastotietoja jaksolta 18.10-27.10. 1985. Finnish Meteorological Institute, Helsinki.

Finnish Meteorological Institute. 1991. Precipitation and snow cover data 1985. Meteorological Yearbook of Finland, 85:3–94.

Granström, U. 1973. Pitfall traps for studying the activity of groundliving spiders (Araneida). Aquilo Ser. Zool., 14:93–98.

Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. Ann. Zool. Fennici, 31:203–217.

Haila, Y., I. K. Hanski & S. Raivio. 1987. Breeding bird distribution in fragments of coniferous taiga in southern Finland. Ornis Fennica, 64:90–106.

Haila, Y., I. K. Hanski, J. Niemelä, P. Punttila, S. Raivio, & H. Tukia. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Ann. Zool. Fennici, 31:187–202.

Hansson, L. 1992. Landscape ecology of boreal forest. Trends in Ecology and Evolution, 7:299–302.

Hauge, E. & R. Wiger. 1980. The spider fauna (Araneae) from 12 habitats in the Vassfaret region, southeastern Norway. Fauna Norvegica, Ser. B., 27:60–67.

Heydemann, B. 1961. Untersuchungen über die Aktivitäts- und Besiedlungsdichte bei epigäischen Spinnen. Verh. Deutschen Zool. Ges. Saarbrücken, 1961:538–556.

Huhta, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. Ann. Zool. Fennici, 2:260–301.

Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fennici, 8:483–542.

Hurlbert, S. H. 1971. The non-concept of species diversity: A critique and alternative parameters. Ecology, 52:577–586.

Itämies, J. & M-L. Jarva-Kärenlampi. 1987. Phenology of wolf spiders (Araneae, Lycosidae) at Pukkila, Central Finland in 1980. Memoranda Soc. Fauna Flora Fennica, 63:73–80.

Itämies, J. & M-L. Jarva-Kärenlampi. 1989. Wolf spiders (Araneae, Lycosidae) on the bog at Pukkila, Central Finland. Memoranda Soc. Fauna Flora Fennica, 65:103–108.

Jennings, D. T., M. W. Housewaert, C. D. Dondale, & J. H. Redner. 1988. Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. J. Arachnol., 16:55–70.

Koponen, S. 1972. On the spiders of the ground layer of a pine forest in Finnish Lapland, with notes on their diurnal activity. Rep. Kevo Subarctic Res. Stat., 9:32–34.

Koponen, S. 1975. Spider populations in a subalpine birch forest. Pp. 66–72, *In* Ecological studies. Analysis and synthesis, vol. 17. Fennoscandian tundra ecosystems, part 2. (F. E. Wielgolaski, ed.). Springer-Verlag, Berlin.

Koponen, S. 1976. Spider fauna (Araneae) of Kevo area, northernmost Finland. Rep. Kevo Subarctic Res. Stat., 13:48–62.

Korsmo, H. 1991. Conserving coniferous forest in Norway – a critical time for international environmental obligations. Ambio, 20:238–243.

Loreau, M. 1985. Annual activity and life cycles of carabid beetles in two forest communitites. Holarct. Ecol., 8:228–235.

McIver, J. D., G. L. Parsons & A. R. Moldenke. 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian J. For. Res., 22:984–992.

Mikkola, K. 1991. The conservation of insects and their habitats in northern and eastern Europe. Pp. 109–119, *In* The conservation of insects and their habitats. (N. M. Collins & J. A. Thomas, eds.). Academic Press, London.

Niemelä, J., Y. Haila, E. Halme, T. Pajunen, & P. Punttila. 1989. The annual activity cycle of carabid beetles in the southern Finnish taiga. Ann. Zool. Fennici, 26:35–41.

Niemelä, J., Y. Haila, E. Halme, T. Pajunen, & P. Punttila. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. J. Biogeogr., 19:173–181.

Niemelä, J., Y. Haila, E. Halme, T. Lahti, T. Pajunen & P. Punttila. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. Ann. Zool. Fennici, 25:107–119.

Niemelä, J., E. Halme, T. Pajunen & Y. Haila. 1986. Sampling spiders and carabid beetles with pitfall traps: the effect of increased sampling effort. Ann. Entomol. Fennici, 52:109–111.

Niemelä, J., D. Langor & J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Cons. Biol., 7:551–561.

Niemelä, J., J. R. Spence, D. Langor, Y. Haila & H. Tukia. 1994a. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. Pp. 29–50, *In* Perspectives in insect conservation. (K. Gaston, M. Samways & T. New, eds.). Intercept Publications, Andover.

Niemelä, J., H. Tukia & E. Halme. 1994b. Carabid assemblages in southern Finnish taiga: a survey in unmanaged forest. Ann. Zool. Fennici, 31:123–129.

Pajunen, T. 1988. Metsien pirstoutumisen ja metsiköiden iän vaikutus maaperähämähäkkien esiintymiseen havumetsissä Pohjois-Hämeessä. Unpubl. MSc. thesis, Dept. Zoology, Univ. Helsinki.

Palmgren, P. 1972. Studies on the spider populations of the surroundings of the Tvärminne Zoological Station, Finland. Commentationes Biologicae, 52: 5–133.

Palmgren, P. & O. Biström. 1979. Populations of Araneae (Arachnoidea) and Staphylinidae (Coleoptera) on the floor of a primeval forest in Mäntyharju, southern Finland. Ann. Zool. Fennici, 16: 177–182.

Topping, C. J. 1993. Behavioural responses of three linyphid spiders to pitfall traps. Entomol. exp. appl., 68:287–293.

Topping, C. J. & K. D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. J. Appl. Ecol., 29:485–491.

Tretzel, E. 1954. Reife- und fortpflanzunszeit bei spinnen. Z. Morph. u. Ökol. Tiere, 42:634–691.

Väisänen, R. & O. Biström. 1990. Boreal forest spiders and the preservation of biotic diversity: results from Finnish primeval forests. Acta Zool. Fennica, 190:373–378.

Westerberg, D. 1977. Utvärdering av fallfällemetoden vid inventering av fält- och markskiktetes lägre fauna (with English summary). Statens Naturvårdsverk, PM 844, VINA Rapp. 5. Stockholm. 72 pp.

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